THE ACARIDAE: A RECAPITULATION
(Acarina: Sarcoptiformes)[1]

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Although the mite family Acaridae is a comparatively small one as regards numbers of species, it is nevertheless one of the most successful groups of animals on earth. Through their unique methods of dispersal, omnivorous food habits and phenomenal reproductive rate, acarids have become well established throughout most of the world. Several species are found commonly in stored grain and grain products where they cause injury by their feeding and by creating, in many instances, difficult contamination problems. Preserved meats, cheeses, bulbs and dried fruits also are liable to infestation by acarids. The majority of species, however, are found living as saprophytes or fungivores in soil, litter, or in the nests of mammals or birds.

The Acaridae may be described as opaque, weakly sclerotized mites ranging in size from 400 to 2000 microns, and completely lacking in respiratory and complex sensory structures. The gnathosoma (fig. 1) is small and compact, with a pair of maxillary palpi closely appressed to the hypostome. The chelicerae are the most prominent gnathosomal feature, being heavy and coarsely chelate distally. The idiosoma is divided by a transverse apodemal suture into a propodosomal and hysterosomal area, each of which bears two pairs of legs in the nymphal and adult stages. The propodosoma has a weak anterior dorsal plate which is all but lost in many species and a more or less constant series of dorsal setae and sensory organs. The rostral setae (fig. 1, r.) are inserted at the anterior edge of the dorsal plate. They usually are quite strong and may or may not be weakly pectinate. The cervical setae (fig. 1, c.) may be found either at the anterior lateral corners of the dorsal plate or on the mediolateral borders of the plate. They generally are small and may be pectinate. The inner and outer propodosomal setae (fig. 1, i.p., o.p.) are inserted transversely across the posterior portion of the

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propodosoma. These setae are highly variable and, in some species, the inner pair may be reduced or absent. Grandjean's organ (fig. 1, x) is a tiny propodosomal structure that is thought to be sensory in function. The organ assumes a tree-like form in some acarids and lies in a body depression just anterior to coxae I, where it often is difficult to detect. In other species it is a seta-like projection which is easily seen. Posterior to Grandjean's organ is a pseudostigmatic spine (fig. 1, p.o.) which may be pectinate or smooth. The dorsum of the hysterosoma commonly bears ten pairs of setae, with reduction occurring in certain genera. Three pairs of humeral setae are found on the anterolateral portion of the hysterosoma (fig. 1, o.h., i.h., m.h.). The inner humeral setae always are the shortest of the three when all are present. Both the middle and inner pairs are completely lost in some species. The lumbar setae (fig. 1, l_1, l_2, l_3) occupy the middle area of the hysterosoma. Only the third lumbars are found in virtually all acarids. As many as seven pairs of setae may be inserted at the posterior margin of the hysterosoma. These are the marginal and all but one of the sub-marginal setae (fig. 1, mg., smg.). Although inserted ventrally, the post-anal setae (fig. 1, p/a) are considered by many authors to be a part of the marginal-submarginal setal complex.

Ventrally, epimera I are fused at the midline, while epimera II-IV are free medially (fig. 2a, op). The genital opening of the female lies between coxae III and IV while that of the male (fig. 2b) usually is found between coxae IV. Two pairs of genital discs flank the genital area in both sexes, and a copulatory sucker is located on either side of the male anal slit. The ventral setae are fairly constant and are considered to be of little importance taxonomically.

While most mites have six-segmented legs, acarids have only five. It is generally assumed that the trochanter has been lost and that the coxa is joined directly to the femur. Possibly, however, the true coxal segments have become fused with the venter, with only the epimera to mark their former positions. Thus the so-called coxa of acarids may, in reality, be the trochanter. Tarsus I (fig. 4) bears several setae, some of which are sensory in function. Nesbitt (1945) has emphasized the importance of these setae in determining phylogenetic development of acarid genera. Tarsus IV of the male bears two (occasionally

one) raised suckers (fig. 2c) on its dorsal surface, which serve to hold the female during copulation. All tarsi terminate in a sessile empodial claw which may be seated in a membranous caruncle. In the genus *Lardoglyphus*, true claws persist in the females, while the male of only one species, *L. zacheri* Oudemans, retains true claws on tarsi I and II.

Taxonomically the Acaridae has proven a confusing problem to the several acarologists who have studied them. Despite the efforts of such well-qualified persons as Berlese, Canestrini, Banks and Oudemans, the systematics of the Acaridae remained enigmatic until relatively recently. It is not surprising that errors occurred in the early works on this group. Lack of clear-cut taxonomic characters coupled with inadequate optical equipment resulted in a number of artificial and highly unstable systems of acarid classification. Rather than treating the Acaridae as a natural, integrated group, many early workers expressed relationships on a suprafamilial basis, creating families on the strength of what we now consider to be tribal or generic characters.
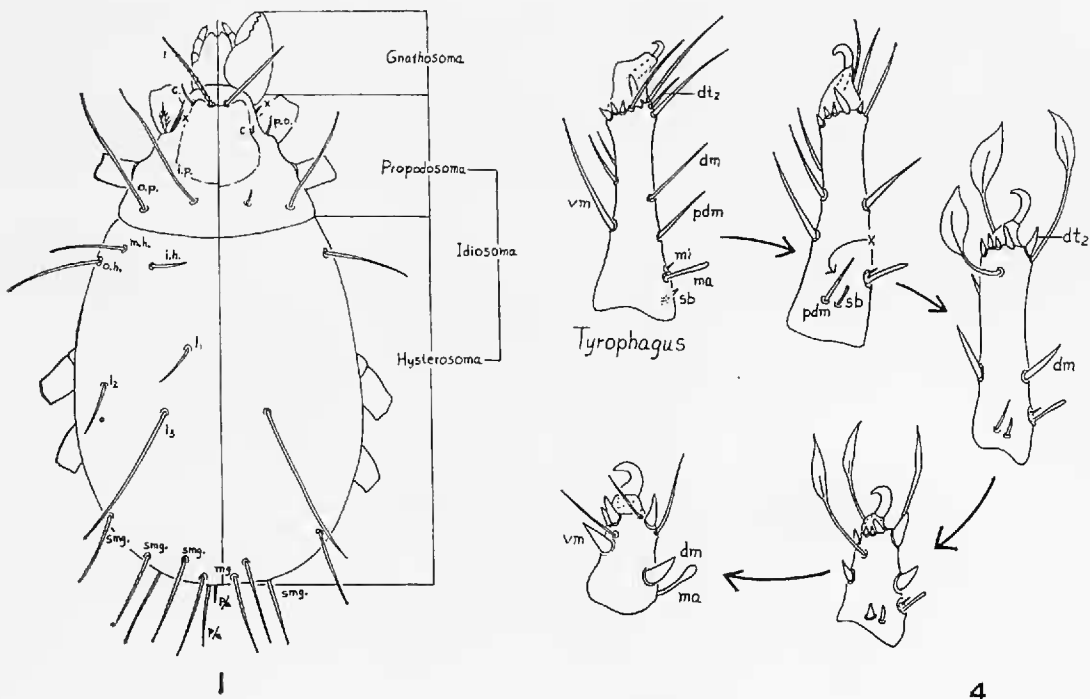
EXPLANATION OF FIGURES

Fig. 1. Diagrammatic representation of the dorsum of an acarid mite, showing extremes in body setation. Fig. 4. Variations in tarsi I of acarid mites, showing developmental trends in setation and segmental length. Vm—ventral median seta; sb—sub-basal seta; ma—macrosense seta; mi—microsense seta; pdm—postdorsal median seta; dm—dorsal median seta; dt₂—second dorsal terminal seta (Adapted from Nesbitt 1945).

The ensuing confusion in species separation led to numerous synonymies, many of which are yet to be resolved.

Realizing the inherent artificiality in the existing systematic concepts, Zakhvatkin (1937, 1940) presented a scheme of acarid classification in which the family Acaridae (then Tyroglyphidae) was extended so as to include several families of earlier authors. Zakhvatkin divided the acarids into two sub-families, both of which were further divided into tribes and genera. He separated his subfamilies through the relative positions of the cervical setae, size and condition of body and tarsal setae, size of the empodial claw, and the presence or absence of a caruncle. Tribal and generic characters were similar to those used later by Nesbitt (1945), with the position and modification of setae on tarsus I being of major importance in the separation of both tribes and genera. The resulting classification was, to quote Nesbitt, "the most satisfactory yet devised for demonstrating relationships in the family." The almost universal acceptance of Zakhvatkin's work by subsequent authors on the Acaridae tends to support Nesbitt's statement.

In 1955, Yunker proposed a classificaton of the supercohort Acaridiae, the group in which the Acaridae occurs. He observed that a natural separation of parasitic and non-parasitic forms could be justified on morphological grounds. Yunker divided the Acaridiae into the cohorts Acaridia (free-living forms), Psoroptidia (parasitic forms), and Ewingidia, a monogeneric intermediate form possessing morphological attributes of both the Acaridia and Psoroptidia. The presence of genital suckers in the Acaridia served to separate it from the remaining cohorts.

The Acaridia comprises four superfamilies (fig. 3), of which only the Acaroidea and the Anoetoidea possess the well-developed empodial claw so typical of members of the family Acaridae. The Anoetoidea differs from the Acaroidea, however, in usually having a transverse rather than a longitudinal genital slit, and in having highly modified palpi (Hughes 1958; Scheucher 1957).

While some authors prefer to think of the Saproglyphidae and Glycyphagidae as subfamilies in the family Acaridae (Türk and Türk 1957), these groups ordinarily are considered to have individual familial status. Unlike typical acarids which possess sessile claws, both saproglyphids and glycyphagids have distinct

pretarsi. In neither group do the males have anal or tarsal suckers as found on male acarids.

As presently conceived, the Acaridae consists of two sub-families — the Acarinae Nesbitt and the Rhizoglyphinae Zakhvat-kin. Structurally the Acarinae are of small size (400-700 microns) and are secondarily homeomorphic. The propodosomal setae (fig. 1) are well-developed and the legs are slender. The cervical setae are inserted on the anterolateral angles of the dorsal plate. Tarsus I is equal to or longer than the combined genu and tibia, and the tarsal setae are simple. The claws are quite weak but the caruncles are strong and distinct. The Rhizoglyphinae, on the other hand, are large mites (700-2000 microns) and are secondarily dimorphic, in that many of the body setae of the male are longer than those of the female. Some of the propodosomal setae may be reduced or absent (fig. 1). The cervical setae are inserted on the mediolateral borders of the dorsal plate. The legs are short and stout, with tarsus I rarely as long as the combined genu and tibia. Some of the tarsal setae are absent in rhizoglyphines, while others are modified into stout spines. The claws are robust, and the caruncles are poorly developed or absent.

As mentioned earlier, because of the absence of other major morphological features in the family, a great deal of emphasis has been placed on the setation and shape of tarsi I in the tribal and generic classification of acarids (fig. 4). It is impossible
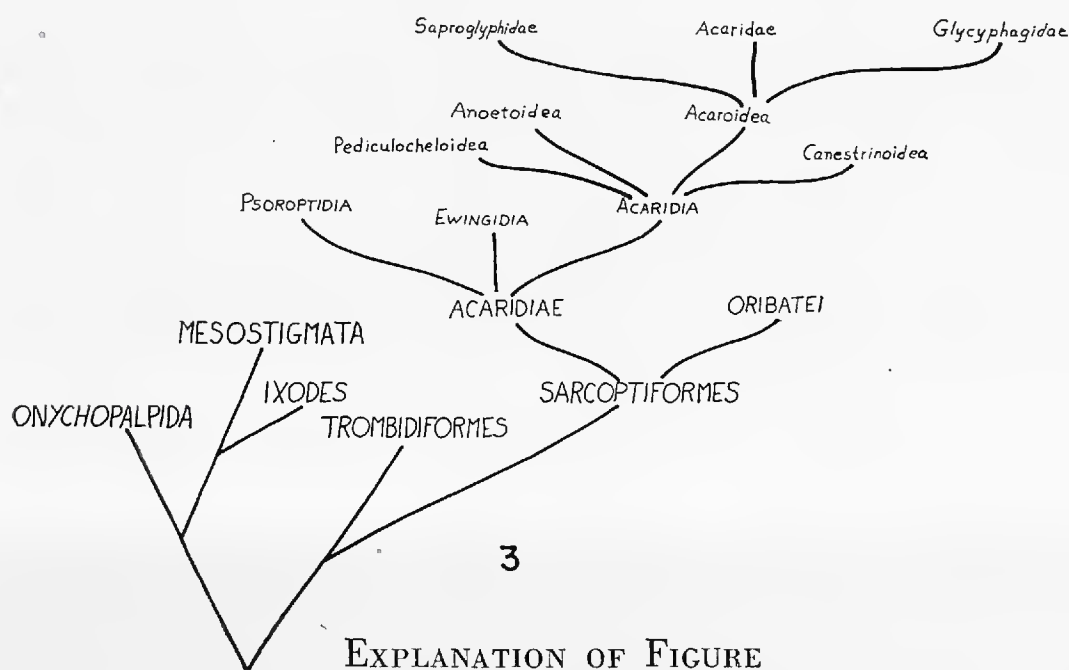
EXPLANATION OF FIGURE

Fig. 3. Derivation of the Acaridae and related groups.

to say what the primitive condition of the tarsus is, but if we can assume the correctness of Oudemans' application of the theory of recapitulation to the Acaridae (1924), the genus *Tyrophagus*, subfamily Acarinae, appears to be the most primitive acarid group. Thus the condition of tarsus I of this genus might be considered primary for the family. Typically, then, tarsus I is equipped with 12 setae, five terminal spines, and an empodial claw and caruncle. In many species, various setae migrate to new positions on the tarsus and often change in shape or size. As these changes become more complex, the tarsal segment itself is seen to become shorter and stouter than in the original primitive condition. Correlated with these progressive alterations is a loss of some of the tarsal setae and an increase in the size of the empodial claw. By using this progression in conjunction with a correlated reduction or loss of body setae (fig. 1), Nesbitt (1945) has traced the relationships and phylogeny of acarid genera. He concludes, among other things, that the Rhizoglyphinae have evolved from the more primitive Acarinae.

Separation of the Acarinae and Rhizoglyphinae is possible on ecological as well as on morphological grounds. Acarids collected from low moisture substrates such as dried fruit or stored grain will almost invariably prove to be members of the subfamily Acarinae, while those acarids found in rotting bulbs, mold or any other high moisture habitat usually will be rhizoglyphines.

While acarids lack apparent defensive structures or the speed necessary to elude the many predators associated with them, still they persist in what oftentimes amounts to astronomical numbers, primarily by out-producing their enemies. Development from egg to adult in some Acaridae may take as little as eight days under conditions of optimum temperature and moisture, and females have been observed to lay over 100 eggs during their lifetimes (Garman 1937).

The acarid life cycle consists of the egg, larval, nymphal and adult stages ordinarily found in other mite groups. The eggs are large and heavily yolked, and are extruded by the female in a haphazard fashion as she crawls over the substrate on which she is feeding. The hatching larva is hexapod rather than octopod as in the succeeding stages. The larva soon becomes quiescent and molts to the first nymphal, or protonymphal, stage. The

protonymph feeds actively for a short time and, after a period of quiescence, transforms to the second nymph. The second nymph may be distinguished from the protonymph by a distinct size differential, as well as by differences in setal patterns. The second nymph resembles the adult in certain respects but sexual
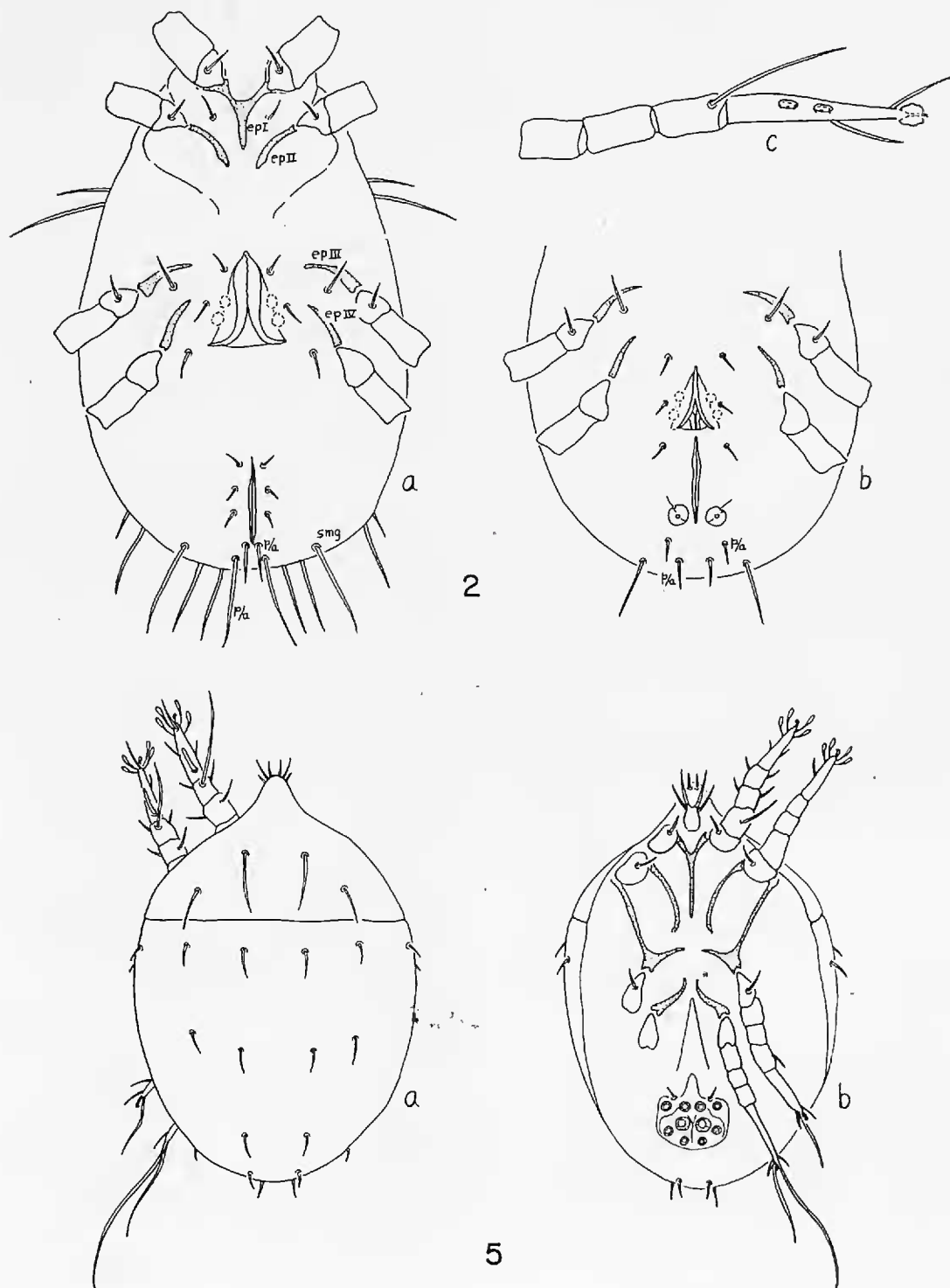
EXPLANATION OF FIGURES

Fig. 2 a. Diagrammatic representation of the venter of female acarid mite. b. Diagrammatic representation of the venter of a male acarid mite. c. Leg IV of a male acarid mite, showing dorsal tarsal suckers. Fig. 5 a. Dorsum of a typical acarid hypopus. b. Venter of a typical acarid hypopus.

characters usually are not clearly defined until the adult molt is attained.

Quite often an extra nymphal stage occurs between the first and second nymphal instars. This form is referred to as the hypopus, or hypopal stage (fig. 5). Because of its time of occurrence in the nymphal sequence, the hypopus is commonly thought of as the second nymphal stage, or deutonymph. When the hypopal stage occurs, the typical second nymphal instar appears at the hypopal molt and is called the third nymph, or tritonymph. Morphologically, there is no observable difference between the typical second instar and the post-hypopal third instar.

The acarid hypopus is peculiar in that it differs so radically from the other acarid instars. It is round or oval in shape, usually darker in color than the preceding or succeeding stages, and is distinctly flattened dorsoventrally. As with the other nymphal forms, eight legs are present but they may be very short. The tarsi often are decorated at their distal ends with a number of elaborate setae. Mouthparts are absent, and the gnathosoma is represented by a tiny anteroventral body projection which may be the developing palpi. A plate of disc-like suckers is located on the ventral side of the hypopus, between or behind the fourth pair of legs. It is by means of these suckers that the hypopus adheres to passing insects, birds or rodents and is carried from one area to another.

Although the hypopal stage has been studied by scores of investigators, the reason or reasons for its sudden and erratic appearance has yet to be defined or proven. According to Michael (1901), eight different theories had been advanced as of the year 1884 concerning the origin of the hypopus. Various workers thought of the hypopus as an itch mite, a separate family of adult Acarina, an immature stage of the predatory genus *Gamasus*, an external parasite, or the male, or male and female, mites of the genus *Tyroglyphus*. In his presidential address before the British Microscopical Society in 1894, Michael described the observations of one worker, who decided that the hypopus was "a ferocious creature which attacked other mites from below, ate its way in, and then devoured its host, leaving only the skin." As pointed out by Michael, the absence of mouthparts in hypopi did not seem to trouble the investigator. Haller (1880) suggested that the hypopus is a protective covering which is produced

when the immediate food supply is exhausted and travel to a new location is necessary. Megnin (1873, 1874) believed the hypopus to be a heteromorphous adventitious nymph which develops only when adverse environmental conditions forces its dissemination. Michael confirmed Megnin's observations on the origin of the hypopus but found that formation of the hypopal stage is not necessarily dependent on environmental conditions. Other experimenters have attributed hypopus formation to moldy or dirty food media (Sokolov 1935; Scheucher 1957), to some unknown "innere Faktoren" (Türk and Türk 1957), or to the presence of two distinct types of nymphs in an average population, one of which will transform to hypopi regardless of environmental conditions, and one which passes into the hypopal stage only when deprived of suitable food (Schulze 1924). Türk and Türk (1957) and Scheucher (1957) feel that lack of moisture in the habitat is a factor which is of primary importance only in that the lack of moisture in the food medium prevents feeding, which in turn leads to hypopal formation.

It can be seen, therefore, that the hypopus question is still open to debate. Until an explanation can be found for this phenomenon, it may be assumed that the hypopus is a form primarily adapted for dissemination and for resistance to environmental inconstancies.

The hypopal stage is by no means limited to the Acaridae. The Saproglyphidae and Glycyphagidae in the Acaroidea, and the Anoetidae in the Anoetoidea have hypopal forms, as do certain of the feather mites in the superfamily Analgesoidea. Further biological studies probably will reveal that hypopi occur also in other Acaridae.

The purpose of this paper has been to summarize some of the more important taxonomic and biological aspects of the Acaridae. It should be realized that, because of the introductory nature of this discussion, many of the incidental phenomena relating to the family have not been included. Much has already been learned, but the Acaridae still offer a major challenge in the field of acarological research.

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